THE BULLETIN OF
Mathematical
BIOPHYSICS

JUNE 1946

IMPORTANT ANNOUNCEMENT

The increase in the output of papers in the field of mathematical biophysics makes it difficult to insure prompt publication without an increase in the size of the journal. Therefore, the Bulletin of Mathematical Biophysics inaugurates the following service:

Upon acceptance of a paper, the Editor, if necessary, will ask the author to shorten the paper to an extent dictated by the requirements of a reasonably prompt publication. The shortening should in no case reduce the paper to a mere abstract. Such a shortened paper will be published within six months or less.

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All papers in the Bulletin which have been thus shortened, will be marked at the end by the symbol MF, followed by a figure, indicating the number of double-spaced typewritten pages of the unabbreviated manuscript.

ON OBLIQUE GROWTH OF TREES UNDER THE ACTION OF WINDS

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It is shown that an inclined regular growth of tree trunks under the action of prevailing winds may be explained as a response of the plant to the mechanical action of the wind, in conformity with the Schwendener theory of shape of plants based on the concept of maximum strength. A possible mechanism of such response is suggested. The condition of maximum strength determines the inclination of the tree trunk on the basis of purely mechanical considerations. A numerical example computed for a palm agrees with observational data.

Since the fundamental investigations of S. Schwendener (1874) (cf. also Holtermann, 1909) a very large amount of experimental material has been published on the relations between mechanical properties of organs of plants and their form and functions; the response of plants to different types of mechanical stimuli has been also investigated (for a review of these topics see W. Schwarz, 1930, 1931 and W. Rasdorsky, 1931, 1937). The ordinary geotropism is a well known type of such response, and other types have been observed directly or induced artificially through various forms of mechanical stress. A tree trunk with an elliptic cross-section having its major axis in the direction of prevailing winds or an increased growth of the trunk and of the roots in the regions which have to resist higher loads (Bernbeck, 1913; Kroll, 1913; Knight, 1803; Preda, 1901; Rasdorsky, 1925); changes in anatomic structure induced by bending, the so-called kamptotropism (Bücher, 1906; Neubert, 1911), exhibiting, for instance, a thickening of cell walls or an eccentric formation of annual rings (Hartig, 1901, pp. 51-57), are all examples of responses of plants to stimuli consisting of mechanical stresses (cf. Bower, *et. al.* 1939, chapter x; Haberlandt, 1924, chapter iv; Ungerer, 1926, pp. 247-251). The biophysical mechanism of such responses may be connected perhaps with the pressure gradient, as it arises, for instance, in bending of a branch through an increase of compressive stresses in one part of the branch and occurrence of tensile stresses in the remaining part (cf. Bernbeck, 1924); the importance of pressure differences for the growth of a tree is suggested by the fact that about 30 to 60 per cent of green wood consists of liquid substances and consequently in the

presence of a pressure gradient, a substantial intercellular flow may occur with a possible change of relative concentrations within single cells, if the permeability of the cell walls exhibits a specific differentiation for the various constituents of the cell.

According to S. Schwendener, the shape of a plant organ having a mechanical function is such as to achieve a maximum of strength. This idea, which was known already to Galileo, has been discussed many times since Schwendener. It is the purpose of the present note to examine this principle of maximum strength in connection with the action of winds on trees.

The mechanical effect of winds on the trunks of trees has substantially two different forms. One occurs when an unusually strong wind bends the tree into a plastic range, so that a very large portion of the tree trunk may acquire permanently an abnormal position, the trunk continues, however, to grow vertically. A beautiful example of such effect is given by L. Preda (1901) in an old juniper having about one-half of its trunk completely horizontal. The same type of effect is shown by the famous "praying" palm of Faridpore in India. This is a date palm whose trunk was bent through 60° by a storm and whose crown exhibits diurnal movements from an erected position in the morning to a lowered position in the evening, the latter effect being a response to environmental changes of physical character (Bose, 1929, chapter xxi). Many other interesting examples of abnormal shapes of trees due to a plastic bending of the trunk may be found in the publications of F. C. Schübeler on the flora of Norway.

A different type of wind effect consists of an oblique growth of the whole tree trunk under the action of prevailing winds. A beautiful photograph of a group of palm trees growing in this way was published recently in the *National Geographic Magazine* (Moore, 1945). [For other examples see e. g. F. C. Schübeler (1885)]. The question arises in connection with this second type of effect whether such regular oblique shape of a trunk should be explained also on the basis of a plastic deformation which has occurred at a certain moment during the life of the tree; or whether under a continuous action of the winds a biological response of the tree could affect its growth in such a manner as to give an oblique shape to the tree. If the latter is the case, we would conclude from Schwendener's theory, by limiting ourselves to the mechanical action of the wind alone, that the inclination of the tree should correspond to a minimum stress. We examine the physico-mechanical characteristics of the tree and its environment in which such explanation is possible.

With reference to the already quoted group of palms we consider a cylinder of length H as an approximate geometric model of the

trunk. Let the horizontal cross-sections of the cylinder be circles of radius R, and the angle of inclination of the cylinder with respect to the vertical axis be v. The wind velocity is variable with the height, particularly near the ground; mathematical formulae expressing this variation are known (s. e. g. Sverdrup, 1939; Brunt, 1941, pp. 251-252) and could be used here; for our approximate computations, however, we assume an average velocity V constant along the entire height H. Theoretical considerations and experimental results indicate that the tangential component with which a wind may act on a circular cylinder is negligible and that the normal component W_t is

$$W_t = N \cos^2(h + v),$$

where h is the angle between the direction of the wind and the horizontal, h being taken positive if the wind is directed upwards and negative if it is directed downwards; N is the force of the wind when it blows perpendicularly to the cylinder (cf. Finsterwalder, 1902, pp. 164-166; Feld, 1945) and is given by the formula (cf. Betz, 1925, pp. 370-373):

$$N = k_t R H V^2,$$

where the coefficient k_t varies from 0.004 to 0.006 for H/R varying from 20 to ∞, N being in kg, V in km/h, R and H in meters. We will use, however, a much higher value of k_t to take into account the roughness of the trunk. Let C be the weight of the crown acting at a horizontal distance c from the top of the trunk. We assume that the force with which the wind acts on the crown is representable by a formula of a well-known type in aerodynamics; viz.:

$$W_c = k_c A V^2 \cos^2 h,$$

where A is the area of the vertical projection of the crown, k_c is a numerical coefficient depending on the shape of the crown and the force W_c is assumed to act horizontally at a vertical distance K from the top of the trunk. Substantially the same type of formula has been used by P. Jaccard (1919) in his studies on trees. Calling the weight of the trunk T, the compressive stress arising at the base of the trunk is due to the compressive force

$$F = T + W_t \sin v + C,$$

and to the bending moment around the center of the base:

$$M = (H/2)(W_t + T \sin v) + (c + H \sin v)C + (K + H \cos v)W_c.$$

The maximum compressive stress S at the base of the trunk is, according to known formulae of the strength of materials,

$$S = (F + 4MR^{-1})/(\pi R^2),$$

so that by the previous formulae

$$\pi R^3 S/H = k_t R V^2 (2H + R \sin v) \cos^2(h + v) + 2(T + 2C) \sin v$$
$$+ 4W_c \cos v + H^{-1}[(T + C)R + 4(cC + KW_c)]. \tag{1}$$

Assuming that the wind force acting on the crown is independent of the inclination v of the trunk, a minimum value of S, if it exists, occurs when v satisfies the equation

$$d(\pi R^3 S H^{-1} V^{-2})/dv = k_t R[\, R \cos v \cos^2(h + v)$$
$$- (2H + R \sin v) \sin 2(h + v)\,] \tag{2}$$
$$+ 2V^{-2}(T + 2C) \cos v - 4k_c A \cos^2 h \sin v = 0.$$

By its physical meaning, the Schwendener principle of maximum strength requires that, as v increases from zero, the function $S(v)$ has a minimum as its first extreme. Therefore, $S(v)$ must be a decreasing function at $v = 0$, and from equation (2) we obtain the condition

$$(\cos h - 8\,l \sin h) \cos h + 2[(T + 2C)/(k_t R^2 V^2)] \leqq 0,$$

where $l = H/(2R)$ is the slenderness of the trunk. We obtain a necessary condition for the fulfillment of the above inequality by changing in it $2C$ into C, but

$$S_0 = (T + C)/(\pi R^2).$$

is the stress S of the same tree when growing vertically in absence of winds. Consequently, we obtain the condition

$$(\cos h - 8\,l \sin h) \cos h + 2\pi S_0/(k_t V^2) < 0. \tag{3}$$

From this inequality we conclude that a sufficient slenderness of the tree, low compressive stresses in the trunk, and high velocities of upwards directed winds, are necessary conditions for the ability of the plant to control its growth under the action of winds in conformity with Schwendener's principle. In the case of downwards directed winds, the above inequality cannot be satisfied because all its terms are positive. Experiments carried out in Germany by O. Lilienthal in various conditions of terrain up to a height of 10 meters show that the average winds are directed upwards with an inclination of about $3\frac{1}{2}°$ to the horizontal (Betz, 1925, p. 367). With such small value of h, normal trees cannot satisfy the inequality in question. In exceptional terrains, however, as, for instance, in mountains or on sea beaches, the direction of the wind may be sufficiently steep or its velocity sufficiently high to make a biological response of the tree in the sense of Schwendener's principle possible.

The condition (3) may be written also in the form

$$\sin(2h - a) > [1 + (4\pi S_0)/(k_t V^2)](1 + 64l^2)^{-\frac{1}{2}}, \qquad (4)$$

where

$$\sin a = (1 + 64l^2)^{-\frac{1}{2}} \approx 1/(8l), \qquad (5)$$

l being very large with respect to 1. If we consider the maximum compressive strength of the wood σ_c and introduce the safety factor of the tree $f_0 = \sigma_c/S_0$, corresponding to vertical growth in absence of winds, we have (cf. Opatowski, 1944, pp. 113-114)

$$S_0 = 473 \times 10^4 G/f_0 \text{ kg/m}^2, \qquad (6)$$

where G is the specific gravity of oven dry wood based on the volume in the green state. The right hand side of inequality (4) must be < 1; this gives a condition independent of the direction of the wind;

$$l f_0 k_t V^2 > 74 \times 10^5 G, \qquad (7)$$

which is obtained with the help of equations (5) and (6). The biophysical meaning of conditions (3) and (7) is the same. The aerodynamic coefficient k_t depends on the shape of the tree and on the roughness of the trunk; it is probably not smaller than 0.02. The slenderness l of the trunk may exceed 100. The safety factor f_0 must be high, because it is referred to the action of the weight of the tree alone, and the tree has to resist also strong winds; f_0 may well exceed 100 or 200. The specific gravity G varies between about 0.3 and 0.7. On the basis of these numerical data we may see from relation (7) that an oblique growth of a tree in the sense of Schwendener's principle of maximum strength is possible only in exceptional conditions involving winds of about 50 or 75 km/h at least. The requirement of such exceptionality of conditions is in agreement with common observation. It should be pointed out, however, that our calculations are based on the assumption of a cylindrical tree trunk; a trunk in the shape of a truncated cone, or having some shape of maximum strength could lead to slightly different numerical conclusions. It should be noted also that the conditions of slenderness and of high safety factor are contrasting with each other. For this reason, it is worthwhile to eliminate from relation (7) the product $l f_0$ by means of the radius of the trunk R. This can be done in the following manner: putting $\rho = C/T$ and calling m the ratio of the weight of the green wood to its weight when oven dry, we easily obtain from equation (6)

$$m(1 + \rho) R l f_0 = 2365. \qquad (8)$$

Consequently, from relation (7)

$$m(1 + \rho)GR < 32 \times 10^{-5}k_tV^2 , \tag{9}$$

where, as before, R is in meters, and V in km/h , and the humidity factor m varies between about 1.3 and 2.5. The meaning of inequality (9) is that the effect under consideration may be observed only on thin trees which do not have heavy crowns.

We proceed now to a calculation of the inclination of a tree, on the basis of equations (1) and (2). Consider, for instance, a palm about the size as represented in the already quoted article of W. R. Moore: $R = 0.075$ m and $H = 15$ m , which corresponds to a slenderness of $l = 100$, $\rho = 0.1$, $A = 3$ m²; assume for the specific gravity G and for the humidity coefficient m the values given by L. J. Markwardt and T. R. C. Wilson (1935) for a Florida palm: $G = 0.37$, $m = 2.34$. This corresponds to a weight of the trunk and of the crown of $T = 229.5$ kg, $C = 22.95$ kg. Equation (8) gives the safety factor corresponding to a vertical growth of the tree in the absence of winds: $f_0 = 122.5$. Putting $k_t = 0.04$, the minimum value of V for which the condition (9) is satisfied is slightly less than 75 km/h. We assume $V = 80$ km/h, although much higher wind velocities have been also observed (cf. Feld, 1945). Equations (4) and (5) give the minimum value of wind inclination for which the effect may be observed: h is somewhat above 30°. We take $h = 38°$. Assuming an aerodynamic coefficient for the crown of $k_c = 0.0005$, which is about ten times smaller than for a circular plate, we obtain the force of the wind acting on the crown $W_c = 5.96$ kg. With these values the equation (2) for the inclination of the tree derived from Schwendener's principle of maximum strength is

$$\cos v \cos^2(38° + v) - (400 + \sin v) \sin(76° + 2v)$$
$$+ 382.5 \cos v - 16.56 \sin v = 0 ,$$

whose numerical solution gives $v \cong 21\frac{1}{2}°$. This value is probably slightly smaller than the inclination of the palms in the photographs of W. R. Moore. However, we have neglected the yielding of the ground.

It is convenient now to calculate the actual safety factor of the tree, in these conditions, and to see how much it gains through the inclined growth. The compressive strength of wood is much higher in pure bending than in pure compression. Formulae of L. J. Markwardt and T. R. C. Wilson give the compressive strength in compression σ_c and in bending σ_b (cf. Opatowski, 1944):

$$\sigma_c = 473 \times 10^4 G , \qquad \sigma_b = 1237 \times 10^4 G^{5/4} \tag{10}$$

in kg/m². Equation (1) gives the actual compressive stress S: the

terms of the right hand side of equation (1) due to pure compression are

$$k_t R^2 V^2 \sin v \cos^2 (h + v) + H^{-1} R (T + C),$$

the remaining terms being due to pure bending. We put the compressive stress at the base of the trunk in the form

$$S = S_c + S_b , \tag{11}$$

where S_c and S_b represent respectively the parts due to pure compression and to pure bending, both under the combined action of the weight of the tree and of the wind. We take $c = K = 0$, that is, we assume that the weight of the crown and the resultant wind force acting on the crown pass through the top of the trunk (cf. the photographs of W. R. Moore); these forces do not affect sensibly the result in any way. We obtain from equation (1), using our numerical values,

$$\left.\begin{array}{lll} S_c = 1.4; & S_b = 404.8 & \text{for } v = 0 , \\[2mm] S_c = 1.4; & S_b = 269.6 & \text{for } v = 21\tfrac{1}{2}° \end{array}\right\} , \tag{12}$$

the units being kg/cm². It is seen that S_c is negligible with respect to S_b, so that in calculating the strength the second formula (10) can be used and the safety factor is $f = \sigma_b/S$. Using equations (11) and (12), we obtain $f = 0.88$ for $v = 0$, that is, assuming our tree is vertical, and $f = 1.32$ for an inclined growth of the same tree according to Schwendener's principle of maximum strength. The 50% of reduction of stress achieved through an appropriately inclined growth is here of a substantial importance for the tree, since it cannot live with $f < 1$. The safety factor of 1.32 is not very high, it is calculated, however, for a strong wind, and it should also be kept in mind that our theory is based on a cylindrical model of a tree, which is very inefficient from the viewpoint of strength. A model with a suitably variable cross-section would yield a higher value of f. Such a model could be determined by combining the ideas of this paper with a theory developed by M. Esser (1946) which gives a shape of a trunk of maximum strength. The latter, however, should be extended to include the action of the wind on the trunk.

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FURTHER CONTRIBUTIONS TO A PROBABILISTIC INTER-PRETATION OF THE MATHEMATICAL BIOPHYSICS OF THE CENTRAL NERVOUS SYSTEM

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Following a previous paper, equations are derived for the most probable time of firing of an efferent neuron in terms of the intensity E of excitation of the afferent pathway, when E is either constant or any given function of time. The equations are not differential equations, but in integral form. It is suggested that ε, correspondingly j, represent the number of excitatory, correspondingly inhibitory, terminal bulbs excited within the period of latent addition at a given most probable time. The relation between the suggested theory and the old one, based on differential equations for ε and j is discussed.

In a previous paper (Rashevsky, 1945b) we suggested an interpretation of the ε and j factor as the number of excitatory or inhibitory terminal bulbs, which is most likely to be excited simultaneously at a given time t. We suggested a non-linear differential equation which reduces as a very rough first approximation to the standard equation for ε and j. The validity of this equation is, however, rather dubious from the point of view of theory of probability.

In the present paper we shall derive some more rigorous probabilistic equations. We shall find that a closed finite expression for the excitatory, correspondingly inhibitory, factor is thus obtained directly, without any recourse to differential equations. For those used to handling the problems of the mathematical theory of the central nervous system in the standard way, based on the differential equations for ε and j, this may appear strange. But we must remember that after all a differential equation is only a mathematical expedient, which possesses some heuristic value. Neither in physics nor in any other mathematical natural science do we ever test experimentally a differential equation directly, but only some finite expressions derived from the differential equation. In many cases, as in diffusion problems, eletrodynamics, hydrodynamics, the differential equation has the advantage of a greater generality. But in some cases, as, for instance, in the case of central excitation, we really do

not gain anything mathematically by using the differential equation

$$\frac{d\varepsilon}{dt} = AE(t) - a\varepsilon,$$ (1)

instead of its general integral

$$\varepsilon(t) = e^{-at} \left[\varepsilon_0 - A \int_0^t E(t) e^{at} \, dt \right].$$ (2)

Both give us ε as a function of t for any prescribed $E(t)$.

Consider the same set-up as before (Rashevsky, 1945b), namely, an efferent neuron whose threshold in terms of the minimum number of terminal bulbs which must be excited is n_1. Let N afferent fibers synapse with this neuron, each fiber having only one terminal bulb on the neuron. Let $n_1 < N$. Let the average frequency ν of discharge be the same in all afferents and let δ be the period of latent addition.

The probability $P(n)$ for any n fibers to bring their impulses to the efferent neuron within the interval δ is then given (Rashevsky, 1945b) by

$$P(n) = (\delta\nu)^n \frac{N!}{(N-n)!n!}.$$ (3)

We shall call the firing of any n terminal bulbs during the interval δ "event n".

The number N varies with the intensity E of the afferent excitation, and therefore for a varying E the number N is a function of time t.

The passing of each interval of time δ may be considered as a trial, and the probability of the event n to occur during a given trial is then given by equation (3). During the i-th consecutive trial, that is, in the i-th interval δ after the beginning of the afferent excitation, the number N has the value N_i, and hence $P(n)$ is a function of both i and n, which may be written $P_i(n)$.

The probability of the event n to occur once and only once during m trials, when its probability to occur during the i-th trial is equal to p_i, is given by

$$p(1, m) = p_1(1 - p_2) \cdots (1 - p_m)$$
$$+ (1 - p_1) p_2 (1 - p_3) \cdots (1 - p_m) + \cdots.$$ (4)

The r-th product of the above expression may be written

$$\frac{p_r}{1 - p_r} \overset{i=m}{\underset{i=1}{\Pi}} (1 - p_i).$$ (5)

Consider now the logarithm of the product in expression (5). We have

$$\log \prod_{i=1}^{i=m} (1-p_i) = \sum_{i=1}^{i=m} \log(1-p_i).$$ (6)

The interval δ is very small (about 0.5 ms), and m is therefore usually very large. If t denotes the time corresponding to a given fixed value of m, then

$$t = m\,\delta; \qquad \delta = \frac{t}{m}.$$ (7)

In our case

$$p_i = P_i(n).$$ (8)

If, as is usually the case, $P_i(n) = p_i << 1$, we may expand the logarithms in expression (6), preserving only linear terms, and thus obtain

$$\log \prod_{i=1}^{i=m} (1-p_i) = \sum_{i=1}^{i=m} \log(1-p_i) = -\sum_{i=1}^{i=m} p_i.$$ (9)

For very large values of m, the above may be approximated by

$$-\int_0^t p(\tau)\,d\tau,$$ (10)

where t denotes the fixed time considered, and τ, the integration variable, is the variable time, of which $p(\tau)$ is now a function. We have

$$p(\tau)\,d\tau = p_i.$$ (11)

Hence

$$\prod_{i=1}^{i=m} (1-p_i) = \exp\left[-\int_0^t p(\tau)\,d\tau\right].$$ (12)

Now the fraction $p_r/(1-p_r)$ in expression (5) becomes simply $p(\tau)\,d\tau$. Hence every term of the sum in expression (4) is now equal to

$$\left\{ \exp\left[-\int_0^t p(\tau)\,d\tau\right]\right\} p(\tau)\,d\tau,$$ (13)

and therefore, writing $p(t)$ for $p(1, m)$:

$$p(t) = \left\{ \exp\left[-\int_0^t p(\tau)\,d\tau\right]\right\}\int_0^t p(\tau)\,d\tau.$$ (14)

For $p(\tau) = \text{const.} = p$, this reduces to

$$p(t) = pte^{-pt}.$$ (15)

The quantity $p(t)$ has a maximum for

$$t = \frac{1}{p},$$ (16)

or, using equations (8) and (11) and putting $p = p_i$, $d_\tau = \delta$:

$$t = \frac{\delta}{P_i(n)},$$ (17)

which is identical with equation (2) of the previous paper (Rashevsky, 1945b).

If the condition $p_i << 1$ is not satisfied, we must evaluate the sum (4) directly. For the case $p_i = \text{Const.} = p_0$, equation (4) reduces to:

$$p(1, m) = mp_0(1 - p_0)^{m-1}.$$ (18)

This has a maximum for

$$m = -\frac{1}{\log(1 - p_0)}.$$ (19)

For very small values of p, equation (19) reduces to

$$m = \frac{1}{p_0},$$ (20)

which, because of relations (7) and (11), is identical with expression (16).

Now let us ask for what value of t the probability $p(t)$ has a maximum in the general case, given by equation (14). We have

$$\frac{dp(t)}{dt} = p(t) \exp\left[-\int_0^t p(\tau) d\tau\right]$$

$$-\left\{\int_0^t p(\tau) d\tau\right\} p(t) \exp\left[-\int_0^t \frac{p(\tau) d\tau}{t}\right].$$ (21)

The requirement

$$\frac{dp(t)}{dt} = 0$$ (22)

gives

$$p(t)\left\{1 - \int_0^t p(\tau) d\tau\right\} \exp\left[-\int_0^t p(\tau) d\tau\right] = 0,$$ (23)

or

$$\int_0^t p(\tau)\, d\tau = 1.$$

(24)

For $p(\tau) = \text{Const.} = p$, this reduces to equation (16).

The number N is a function of the intensity $E(\tau)$ of the afferent excitation. Hence N is a given function $N(\tau)$ of the time. Because of equations (3), (8), and (11), together with $d\tau = \delta$, the quantity $p(\tau)$ is thus a known function of the variables τ and n; thus $p(\tau) = \phi(\tau, n)$. Hence for every value of n, equation (24) gives us the most probable time for which n bulbs will be *once and only once* excited all within the interval δ. Putting $n = n_1$, we find the most probable time for the efferent neuron to fire once and only once.

For a constant E, the value of N is constant, and the most probable time of firing of the efferent neuron is given by

$$t_1 = \frac{\delta}{P(n_1)} = \frac{\delta}{(\delta \nu)^{n_1}} \frac{(N - n_1)!\, n_1!}{N!}.$$

(25)

In actual experimental determination of reaction times, the experiment is repeated many times under constant conditions, but each observation yields a different value of the reaction time. All those values are scattered around a most probable one, which is considered as *the* reaction time. We may therefore consider equation (25) as giving the reaction time as a function of the intensity of the stimulus S in a simple reflex arc. For large values of N, and for $N >> n_1$, that is, for stimulations highly exceeding the threshold, t_1 varies approximately as N^{-n_1}. Hence, if $n \propto E \propto S$, then $t_1 \propto S^{-n_1}$. Actually, it is found (Landahl, 1939, Rashevsky, 1940, chap. ix) that $t_1 \propto S^{-1}$ and sometimes even $t_1 \propto (\log S)^{-1}$. Since most likely $n_1 >> 1$, the expression (25) leads to a too rapid decrease of t_1 with increasing S, than is compatible with experiment, if $N \propto S$. But actually, as S increases N will tend to a limiting value N_0, the total available number of fibers in the pathway (Rashevsky, 1938, chap. xxv). The $N-S$ curve will rise for large values of S slower and slower. The actual law of variation of N with S depends on the distribution function of the thresholds. Empirically we may try to put

$$N = \frac{aS}{b + S}.$$

(26)

It would be of interest to try how well reaction time data, analysed by H. D. Landahl (1939; Rashevsky, 1940, chap ix) from the point of view of the differential equations ε and j, will agree with

equations (25) and (26) for a proper choice of the constants a, b, and n_1.

The present theory gives us not only the reaction time as a function of the stimulus intensity, but also the frequency of the observed deviations from the most probable value. For a constant stimulus equation (15) gives us directly the probability of a response for any time t.

Equation (24) defines an implicit function $n(t)$. Putting

$$F(n, t) = \int_0^t p(\tau) d\tau = \int_0^t \phi(\tau, n) d\tau, \tag{27}$$

we have

$$\frac{dn}{dt} = -\frac{\dfrac{\partial F}{\partial t}}{\dfrac{\partial F}{\partial n}}. \tag{28}$$

From equation (27) we have, putting

$$\frac{\partial \phi}{\partial n} = \phi_n'; \qquad \frac{\partial \phi}{\partial \tau} = \phi_\tau'; \tag{29}$$

$$\frac{\partial F}{\partial t} = \phi(t, n); \qquad \frac{\partial F}{\partial n} = \int_0^t \phi_n'(\tau, n) d\tau. \tag{30}$$

Hence

$$\frac{dn}{dt} = -\frac{\phi(t, n)}{\displaystyle\int_0^t \phi_n'(\tau, n) d\tau}, \tag{31}$$

or

$$\int_0^t \phi_n'(\tau, n) d\tau = -\frac{\phi(t, n)}{\dfrac{dn}{dt}}. \tag{32}$$

Taking partial derivatives of both sides with respect to t and rearranging, we find

$$\phi(t, n) \frac{d^2 n}{dt^2} - \phi_n'(t, n) \left(\frac{dn}{dt} \right)^2 - \phi_t'(t, n) \frac{dn}{dt} = 0. \tag{33}$$

This is the differential equation determining the number of terminal bulbs firing within an interval δ as a function of the most probable time of that event. For practical purposes the integral expression (24) is much simpler.

The number n may be identified with ε, correspondingly j. If equations (25) and (26) can represent intensity-time relations in reaction times for constant stimuli, then the present theory is *empirically* equivalent to the standard one, because no actual quantitative comparison of theory and experiment for variable stimuli has been made. To what extent the two theories may be equivalent mathematically, can be decided only by a further mathematical study. If we set the right side of equation (2) equal to h, for a given $E(t)$ it determines the firing time t_1 of the efferent neuron. We may compare the roots of this equation with that of equation (24) for $n = n_1$.

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A NOTE ON THE EXCITATION OF NERVE PATHWAYS

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Let S denote the intensity of a stimulus, ν the frequency of discharge of a fiber, and ν_T the integral frequency of discharge of a nerve pathway. The relation between ν_T and S can be derived when the relation between ν and S, as well as the distribution function of the fiber thresholds are given. It is investigated under what conditions the functions $\nu_T(S)$ and $\nu(s)$ will be both of the same exponential form, and it is shown that this can happen only if S exceeds the highest threshold of the pathway.

Peripheral nerve fibers are excited by applying a stimulus of sufficient strength to their receptor organs. For rapidly adapting fibers, a few discharges will occur, and then no further excitation will occur unless the stimulus is increased. For slowly adapting fibers, a steady volley of discharges at a frequency ν sec^{-1} will be evoked for some length of time. Touch receptors are an example of rapid adaptation, while muscle receptors such as the flower spray receptor organ are instances of slow adaptation (Fulton, 1943). We propose here to consider pathways of parallel fibers which are so slowly adapting that they may be approximately considered as non-adapting, all subject to the same stimulus S.

For these fibers, the frequency discharge ν will be given by some functional relation

$$\nu = \phi(S, h), \tag{1}$$

where h, the threshold of the fiber, is the smallest stimulus capable of producing excitation, and the function ϕ is monotonic increasing with S but may have an upper limit. In addition we have

$$\phi(S, h) = 0, \qquad S < h. \tag{2}$$

If we have N_0 fibers in all in the pathway, we define the total frequency of the pathway ν_T as

$$\nu_T = \sum_{i=1}^{N_0} \nu_i. \tag{3}$$

N. Rashevsky (1945) suggests that v_T is the measure of the total excitation E of a pathway. If h' is the lowest threshold in the pathway and $N(h)$, $h \geq h'$ is the distribution function of thresholds in the pathway, then *assuming* that $\phi(S, h)$ is the same function for all the fibers in the pathway, we have

$$v_T(S) = \int_{h'}^{S} \phi(S, h) N(h) dh. \tag{4}$$

Making the assumption that $\phi(S, h)$ is given by

$$\phi(S, h) = \frac{1}{\theta}[1 - e^{-a\theta(S-h)}], \qquad S \geq h \quad \left.\begin{array}{c} \\ \\ \end{array}\right\},$$

$$\phi(S, h) = 0, \qquad S < h \tag{5}$$

a function suggested by N. Rashevsky (1940) as possibly applying to some nerve fibers, equation (4) becomes

$$v_T(S) = \frac{1}{\theta} \int_{h'}^{S} N(h) dh - \frac{e^{-a\theta S}}{\theta} \int_{h'}^{S} e^{a\theta h} N(h) dh. \tag{6}$$

It is of interest to see what conditions would be imposed of necessity on the distribution function $N(h)$ in order that $v_T(S)$ have for all values of S the same form as the function of equation (5) assumed to hold for an individual fiber, i.e., let $v_T(S)$ be given by

$$v_T(S) = k[1 - e^{-b(S-h')}]. \tag{7}$$

Denoting by $M(x)$ and $L(x)$ any two functions satisfying

$$\frac{dM(x)}{dx} = N(x), \qquad \frac{dL(x)}{dx} = e^{a\theta x} N(x); \tag{8}$$

and combining equations (6), (7), and (8), we obtain

$$k[1 - e^{-b(S-h')}] = \frac{1}{\theta}\{M(S) - M(h') - e^{-a\theta S}[L(S) - L(h')]\}. \tag{9}$$

Differentiating both sides of equation (9) with respect to S gives

$$bke^{-b(S-h')} = ae^{-a\theta S}[L(S) - L(h')], \tag{10}$$

hence

$$L(S) - L(h') = \frac{bk}{a} e^{bh'} e^{(a\theta-b)S}. \tag{11}$$

Differentiating both sides of equation (11) with respect to S gives

$$e^{a\theta S} N(S) = \frac{bk}{a} e^{bh'} (a\theta - b) e^{a\theta S} e^{-bS}, \tag{12}$$

from which we obtain, as a necessary condition on the distribution function $N(h)$ in order that ν_T be a function of the same form as the function ϕ of equation (5), the following:

$$N(h) = \frac{bk}{a} (a\theta - b) e^{-b(h-h')}. \tag{13}$$

Now if the function $N(h)$ of equation (13) is introduced into equation (6), the result is a function $\nu_T(S)$, given by

$$\nu_T(S) = \frac{k}{a\,\theta} [(a\theta - b) + be^{-a\theta(S-h')} - a\theta e^{-b(S-h')}]. \tag{14}$$

This function has a different form from the function of equation (7), hence we must conclude that there exists no distribution function $N(h)$ which for all values of S will make $\nu_T(S)$ a function of the form

$k[1 - e^{-b(S-h')}]$ when $\phi = \dfrac{1}{\theta} [1 - e^{-a\theta(S-h)}]$.

Any nerve pathway has a maximum threshold h_m, i.e., $N(h) = 0$ for $h > h_m$. Then for $S > h_m$, equation (6) takes the form

$$\nu_T(S) = A - Be^{-a\theta S}, \tag{15}$$

where A and B are given by the equations

$$\left. \begin{array}{l} A = \dfrac{1}{\theta} \displaystyle\int_{h'}^{h_m} N(h)\,dh = N_0/\theta \\[3mm] B = \dfrac{1}{\theta} \displaystyle\int_{h'}^{h_m} e^{a\theta h}\, N(h)\,dh \end{array} \right\} . \tag{16}$$

If we denote by p the quantity

$$p = \frac{1}{a\,\theta} \log \frac{B}{A}, \tag{17}$$

then equation (15) may be written as

$$\nu_T(S) = \frac{N_0}{\theta} [1 - e^{-a\theta(S-p)}], \tag{18}$$

a function of the same form as the function of equation (5).

Thus for a stimulus S great enough to excite *all* the nerve fibers of the pathway, the total frequency of discharge ν_T of the pathway will depend on S in the same manner as the discharge frequency of an individual fiber. This result is independent of the distribution function $N(h)$.

If h_m is very small, equation (18) may be simplified for values of S reasonably close to h_m by expanding $e^{-a\theta(S-p)}$ and dropping all but the linear terms. We thus obtain

$$\nu_T(S) = N_0 a(S-p).\qquad(19)$$

Applying the mean value theorem for integrals to the second equation (16), we obtain

$$B = e^{a\theta\bar{h}}\frac{N_0}{\theta},\qquad(20)$$

where $\bar{h}$ is between h' and h_m. From equations (20) and (16) we have

$$\frac{B}{A} = e^{a\theta\bar{h}},\qquad(21)$$

hence

$$\bar{h} = \frac{1}{a\,\theta}\log\frac{B}{A} = p.\qquad(22)$$

Thus p is between h' and h_m.

If we assume that $\nu_T(S)$ is a linear function S, i.e.,

$$\nu_T(S) = KS + F,\qquad(23)$$

introducing equation (23) into equation (6) and making use of equation (8) we have

$$KS + F = \frac{1}{\theta}[M(S) - M(h')] - \frac{e^{-a\theta S}}{\theta}[L(S) - L(h')].\qquad(24)$$

Differentiating both sides of equation (24) gives, after rearranging terms,

$$L(S) - L(h') = \frac{K}{a}e^{a\theta S}.\qquad(25)$$

Differentiating both sides of equation (25) gives

$$N(S) = \theta K,\qquad(26)$$

as a necessary condition on the distribution function $N(h)$ in order that $\nu_T(S)$ be linear. On the other hand, if $N(h)$ of equation (26) is introduced into equation (5), we obtain for $\nu_T(S)$

$$\nu_T(S) = K(S - h') - \frac{K}{a\,\theta}[1 - e^{-a\theta(S-h')}].\qquad(27)$$

This function is certainly not linear and at most is approximately zero for values of S close to h'. Thus we may conclude that $\nu_T(S)$ will

not be linear for a very large range of S for any function $N(h)$.

Much work in the mathematical biophysics of the central nervous system is based on the assumption that for the ranges of stimuli considered, ν_T is approximately a linear function of S. We see from preceding results that for this assumption to be valid, it is necessary to assume that the maximum threshold h_m of the nerve pathway is very small and that the quantity $a\theta(S-p)$ be sufficiently small. If $\nu_T(p)$ is close to zero, then equation (18) and the additional condition that $\nu_T = 0$ for $S < p$ corresponds very well to the variation of ν_T with S. If the distribution function $N(h)$ were skewed to the right considerably, then the value of ν_T would be small and would not rise rapidly until h approached very close to p. In such a case as this, we could use equation (19) with good results. Since θ is a measure of the refracting time for nerve fibers in the pathway, we would obtain better results with nerves of very low refractory time.

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TREE TRUNKS AND BRANCHES AS OPTIMUM MECHANICAL SUPPORTS OF THE CROWN: I. THE TRUNK

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The theoretical shape of the trunk of a tree is determined by postulating that the maximum compressive stress due to the action of gravity and wind on an inclined tree is constant for all cross-sections of the trunk. In the general case, the shape is obtained by successive approximations. In some particular cases, the shape is given explicitly.

Introduction. A theoretical study of the shape of tree trunks can be based on various postulates as to its determining cause. It can be based, for instance, on

I. Considerations of sap conduction, where the trunk is considered mainly as a conveyor of metabolic substances.

II. Mechanical considerations, where the trunk is considered mainly as a support of the crown.

III. Considerations of growth, in which the rate of increase in diameter of the trunk is considered more important than the actual diameter at any time.

We cite a few names: N. Rashevsky (1943a, b) studied I and II. S. Schwendener (1909) and I. Opatowski (1944a, b; 1945a) studied II, and P. Jaccard (1919) studied a combination of I and III.

Besides the three factors mentioned above, many other causes influence the shape of trunks. An ideal treatment of the problem of shape would take all factors into consideration, but for the simplicity of the mathematics involved, only one or two factors should be considered at one time. The results so obtained should then be compared with actual data. Experimental data are not yet precise enough to indicate the relative importance of the leading different theories.

In the present and in a subsequent paper, the viewpoint II will be used.

For our study, trees consist of a trunk and a crown, the trunk being the part of the tree located between the ground and the base of its lowest branch, and the crown being the remainder of the aerial part of the tree. When a primary branch is considered, this branch

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will also be separated into two parts, namely, the portion contained between the trunk and the first secondary branch, and the remainder. These two parts will be called the stem and the crown of the branch respectively. We will use the language corresponding to trunks, but it must be kept in mind that our considerations apply also to primary branches because these branches can be considered as very inclined trees attached to the trunk instead of being rooted to the ground.

Trunks are considered to be homogeneous solids with circular symmetry. The whole tree is supposed to have a plane of symmetry. The action of gravity and of wind is considered. The force of wind on the crown is supposed horizontal and in the plane of symmetry of the tree.

By "cross-section z" we mean a cross-section of the trunk by a plane normal to the axis of the trunk, and at a distance z from the base of the trunk. We determine the shape of the trunk by postulating that the maximum compressive stress $\sigma(z)$ on each cross-section equals some constant σ:

$$\sigma(z) = \sigma. \tag{1}$$

Sheering stresses are generally small in comparison to compressive stresses and therefore will not be considered. The assumption
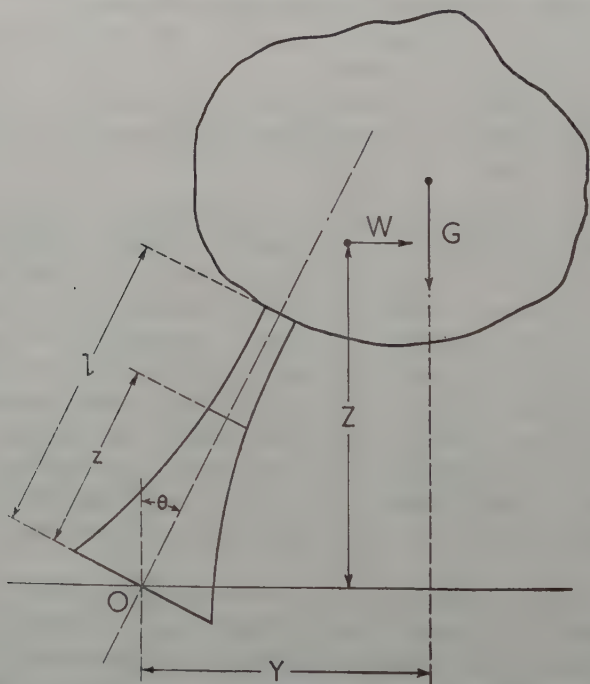

FIGURE 1

(1) could be justified, for instance, as follows:

The shape of a theoretical trunk is such that it can support a pre-assigned crown with the greatest economy of material. Mechanical function or biological activities impose an upper bound σ on the stress allowable in the trunk. The greatest economy of material is obtained by giving a minimum radius to each cross-section. To a decrease of radius corresponds an increase of stress, and the minimum radius is obtained by setting the maximum stress $\sigma(z)$ on each cross-section equal to the upperbound σ.

Instead of assuming a greatest economy of material, equation (1) could also have been justified by assuming a maximum height of the tree, or a greatest safety factor against breakage, or by showing how stress affects growth.

Calculation of the stress. We use the following notations (cf. Figure 1):

$0 =$ point of intersection of axis of trunk with ground
$l =$ length of trunk
$G =$ force of gravity on crown
$W =$ force of wind on crown
$Y =$ horizontal distance from 0 to the line of application of G
$Z =$ vertical distance from 0 to the line of application of W
$z =$ distance from a variable point of the stem to the cross-section through 0
$r(z) =$ radius of cross-section
$\theta =$ angle of inclination of trunk with the vertical
$\omega =$ specific gravity of stem
$\sigma(z) =$ compressive stress at the lowest point of the cross-section at z.

In order to obtain always the maximum stress on the lowest point of each cross-section, we suppose that

$$\theta \geqq 0$$
$$G \cos \theta - W \sin \theta \geqq 0 \qquad (2)$$
$$G(Y - l \sin \theta) + W(Z - l \cos \theta) \geqq 0 .$$

We consider a force F in the vertical plane containing the axis of the trunk and applied to a point of the crown or of the portion of trunk contained between the crown and the cross-section corresponding to a certain z. Denote by F_z the projection of F upon the axis and by $M(F)$ the moment of F with respect to the center of the cross-section. Then the compressive stress due to F at the lowest point of the cross-section z is given by (Timoshenko, 1940, p. 226)

$$\sigma(z) = \frac{F_z}{\pi \, r^2(z)} + \frac{4M(F)}{\pi \, r^3(z)}.$$

When several forces act on the tree, the resulting stress is the sum of the stresses due to the different forces.

We get for the stresses σ_G, σ_T, σ_W, due to the gravity of the crown, to the gravity of the trunk, and to the wind respectively, the following values:

$$\sigma_G(z) = \frac{G \cos \theta}{\pi \, r^2(z)} + \frac{4\,(Y - z \sin \theta)\,G}{\pi \, r^3(z)},$$

$$\sigma_T(z) = \frac{\cos \theta \cdot \omega \cdot \int_z^l r^2(\zeta)\, d\zeta}{r^2(z)} + \frac{4 \sin \theta \cdot \omega \cdot \int_z^l (\zeta - z)\, r^2(\zeta)\, d\zeta}{r^3(z)},$$

$$\sigma_W(z) = \frac{-W \sin \theta}{\pi \, r^2(z)} + \frac{4}{\pi} \, \frac{(Z - z \cos \theta)\,W}{r^3(z)}.$$

The total stress is

$$\sigma(z) = \sigma_G(z) + \sigma_T(z) + \sigma_W(z)$$

$$= \cos \theta \left[\frac{G}{\pi \, r^2(z)} + \frac{\omega \int_z^l r^2(\zeta)\, d\zeta}{r^2(z)} \right]$$

$$+ \sin \theta \left[-\frac{4}{\pi} \, \frac{zG}{r^3(z)} + \frac{4 \, \omega \int_z^l (\zeta - z)\, r^2(\zeta)\, d\zeta}{r^3(z)} \right] \qquad (3)$$

$$+ Y \left[\frac{4}{\pi} \, \frac{G}{r^3(z)} \right] + W \left[-\frac{\sin \theta}{\pi \, r^2(z)} + \frac{4}{\pi} \, \frac{Z - z \cos \theta}{r^3(z)} \right].$$

The last member consists of four terms which consider respectively the gravity for a perfectly vertical tree, the influence of inclination of the trunk, the influence of eccentricity of the crown and the action of the wind.

A numerical example. The purpose of this example is to show the relative importance of the different contributions to the stress $\sigma(z)$, and also to see to what extent our postulate that $\sigma(z)$ is independent of z, see equation (1), is justified. The units used in the calculations are meters and tons.

A complete set of data on any one tree has not been found. Some data of geometrical nature on the "epicea no. 1 de Hasliwald" are given by P. Jaccard (1919, pp. 3-5). The missing data will be

obtained by more or less speculative methods. The height of the tree is 38 meters and the height of the trunk is $l = 15$ meters. The weight of the trunk is calculated by assuming a specific gravity $\omega = 1$ and the weight of the crown is obtained by assuming $\sigma(3) = \sigma(15)$ in the absence of wind and inclination. The force of the wind, $W = 3.5$ tons, is obtained from an estimation made by P. Jaccard for an intensity of wind such that it exerts a force of 50 kg on a plate of one square meter. This is a strong wind of a little less than 100 kilometers per hour. The point of application of W has been taken at the lower third of the crown ($Z = 22$), although Jaccard for some unknown reason, takes it still lower. We get then

TABLE I

Height of cross-section $z =$ meters	Measured diameter of cross-section $2r =$ meters	Area of cross-section square meters	Calculated weight of trunk above considered cross-section Tons	Stress of Gravity Tons per square meter	Stress due to a wind of 50 kg per square meter Tons per square meter
15	.466	.170	.0	18.5	1250
13	.495	.192	.354	18.2	1320
11	.510	.204	.748	19.0	1480
9	.524	.215	1.160	20.0	1610
7	.554	.240	1.610	19.8	1580
5	.588	.270	2.100	19.4	1500
3	.635	.315	2.680	18.5	1330
1	.75	.440	3.390	14.8	900

Calculated weight of the crown:

$$\frac{\text{weight of crown}}{\text{weight of tree}} = \frac{\text{cross-section at 15}}{\text{cross-section at 3}}, \frac{G}{G + 2.68} = \frac{.170}{.315},$$

$$G = 3.14 \text{ Tons}.$$

We will now compare the order of magnitude of the four terms of the last member of equation (3). The first term is of the order of 20 tons per square meter, as shown in the preceding table. We will calculate for what inclination, eccentricity, and wind intensity the other terms of the last member of equation (3) are also of the order of 20.

To calculate θ, we have the equation

$$\sin \theta \left[-\frac{4}{\pi} \frac{zG}{r^3(z)} + \frac{4 \omega \int_z^l (\zeta - z) r^2(\zeta) d\zeta}{r^3(z)} \right] = 20.$$

A rough estimate of the brackets will be obtained by taking in the first term z equal to zero, taking as an average value $r(z) = .30$ meters, and taking the integral equal to

$$\pi \int_1^l \frac{l}{3} r^2(\zeta) d\zeta = \frac{l}{3} \times \pi \int_1^l r^2(\zeta) d\zeta$$

$$= \frac{l}{3} \times \text{mass of the trunk} = 5 \times 3.39 = 17 \text{ meter tons.}$$

We have then

$$\sin \theta \frac{4 \times 17}{.3^3} = 20; \quad \sin \theta = .0075, \quad \theta = \tfrac{1}{2} \text{ degree.}$$

The eccentricity Y is given by the equation

$$20 = Y \frac{4}{\pi} \frac{G}{r^3(z)} = Y \frac{4}{\pi} \frac{3.14}{.3^3} = 150 \, Y, \qquad Y = .13 \text{ meters.}$$

The numbers in the last column of the preceding table are about 80 times larger than those of the preceding column. To get numbers of the same order of magnitude in both columns, we would have to take a wind of intensity $50/80 = .8$ kilograms per square meter. This wind has a velocity of about 12 kilometers per hour.

Conclusions from the numerical example. We see in the table that the stress due to gravity is fairly constant and therefore justifies the postulate $\sigma_G = $ constant [cf. equation (1)]. The stress due to wind has a greater variation. The postulate $\sigma_W = $ constant, is therefore less justified. The quantities σ_G and σ_W have the same defect of being too large in the middle of the trunk. Therefore, a postulate of the form $\sigma_G + k \, \sigma_W = $ constant, where k is a positive constant, and which takes into account a combined action of gravity and wind, is

not more justified by our example than the postulate $\sigma_G =$ constant.

The example shows also that for inclinations greater than half a degree, eccentricities greater than 13 centimeters and wind velocities greater than 12 kilometers per hour, the stresses due to inclination, to eccentricity, and to wind are each greater than the stress in a perfectly vertical tree in a calm atmosphere. It is thus evident that none of all these factors can be neglected.

To show the importance of eccentricity and inclination, we cite a formula found on pages 230-231 of S. Timoshenko (1940):

$$\sigma = \sigma_c \left[1 + 4\frac{d}{r} \right],$$

which gives the maximum stress σ on an arbitrary circular cross-section of the trunk in terms of the stress σ_c in a perfectly symmetric tree of same weight and same radius of cross-section, of the radius r of the cross-section, and the horizontal distance d of the center of gravity of the tree to the center of the cross-section.

Another mechanical factor which may be important but will not be considered, is the elastic stability of the tree.

Theoretical form. A combination of expressions (1) and (3) gives

$$\sigma \, r^3(z) = \omega \cos \theta \, r(z) \int_z^l r^2(\zeta) \, d\zeta +$$

$$4 \, \omega \sin \theta \int_z^l (\zeta - z) r^2(\zeta) \, d\zeta + \qquad (4)$$

$$\frac{G \cos \theta - W \sin \theta}{\pi} r(z) - 4 \frac{G \sin \theta + W \cos \theta}{\pi} z + 4 \frac{GY + WZ}{\pi}.$$

This integral equation can be solved by the successive approximations

$$r_0(z) = \text{arbitrary function};$$

$$\sigma \, r^3{}_{n+1}(z) = \omega \cos \theta \, r_n(z) \int_z^l r^2{}_n(\zeta) \, d\zeta +$$

$$4 \, \omega \sin \theta \int_z^l (\zeta - z) r^2{}_n(\zeta) \, d\zeta \qquad (5)$$

$$+ \frac{G \cos \theta - W \sin \theta}{\pi} r_n(z) - 4 \frac{G \sin \theta + W \cos \theta}{\pi} z + 4 \frac{GY + WZ}{\pi};$$

$$r(z) = \lim_{n \to \infty} r_n(z).$$

The validity of this method of solution can be proved in the usual way, as it is done, for instance, by E. Goursat (1929, chap. xix).

If for all z we have $r_0(z) \leqq r_1(z)$, then the sequence $r_n(z)$ is non-decreasing. To show this, we remark that from $r_0(z) \leqq r_1(z)$ and from inequality (2) it follows that the second member of the middle equation of system (5) is smaller for $n = 0$ than for $n = 1$. A comparison of the first members gives then $r_1(z) \leqq r_2(z)$. Proceeding inductively, we find that $r_n(z) \leqq r_{n+1}(z)$ for each n, which is what we wanted to show. The inequality $r_0(z) \leqq r_1(z)$ is satisfied in particular by $r_0(z) \equiv 0$ and by the functions $r_0(z)$ which we will consider later.

Physical considerations suggest a set of approximations a little different from those given by expressions (5). The approximation $r_{n+1}(z)$ is calculated so as to obtain a constant stress when we take as weight of the trunk not its actual weight, but the value determined by the approximation $r_n(z)$. The equations of these approximations are obtained from expressions (5) by replacing in the second member of the middle equation the first $r_n(z)$ and the last $r_n(z)$ by $r_{n+1}(z)$, while the $r_n(\zeta)$ under the two integral signs are unchanged. This approximation method involves the solution of an algebraic equation of third degree, but does not involve the solution of an integral equation or differential equation.

Solutions for particular cases. The equation (4) will be solved exactly in some particular cases.

I. $\omega = 0$. In other words, the weight of the trunk is negligible. The integral equation (4) reduces then to an algebraic equation of third degree. If in addition we set $\theta = G = 0$, we get

$$r^3(z) = \frac{4W}{\pi \sigma} (Z - z).$$
(6)

Thus when the action of wind alone is considered, our trunk is shaped as a cubic paraboloid with concavity downward.

II. $\theta = 0$, $Y = 0$, $W = 0$. In other words, we have a perfectly vertical tree in the absence of wind. Equation (4) reduces to

$$\sigma r^2(z) = \omega \int_z^i r^2(\zeta) d\zeta + \frac{G}{\pi}.$$
(7)

By differentiation we get

$$\sigma \frac{dr^2(z)}{dz} = - \omega r^2(z),$$

and we obtain as a solution of equation (7)

$$r^2(z) = \frac{G}{\pi\,\sigma}\,e^{\omega(l-z)/\sigma}.\tag{8}$$

This exponential form has been considered by many authors and is sometimes in fairly good agreement with observations.

We obtain also a simple second approximation if we take $\theta = 0$, $Y = 0$, $W = 0$ for our first approximation and only $\theta = 0$ for our second approximation. We get then, when $r_0(z)$ is given by equation (8),

$$r^3{}_1(z) = r^3{}_0(z) + W\,\frac{4}{\pi\,\sigma}\,(Z-z) + Y\,\frac{4G}{\pi\,\sigma}$$

$$= \left[\frac{G}{\pi\,\sigma}\right]^{3/2} e^{3\omega(l-z)/2\sigma} + \frac{4W}{\pi\,\sigma}\,(Z-z) + \frac{4GY}{\pi\,\sigma}.$$

We see that this approximation $r^3{}_1(z)$ is the sum of the exact values of $r^3(z)$ obtained by considering the action of gravity alone, as in equation (8), of wind alone, as in equation (6), and of eccentricity alone.

III. $\theta = \dfrac{\pi}{2}$, $W = 0$. In other words, we are studying a hori-

zontal branch in the absence of wind. Then equation (4) reduces to

$$\sigma\,r^3(z) = 4\,\omega\int_z^l (\zeta-z)\,r^2(\zeta)\,d\zeta + \frac{4G}{\pi}\,(Y-z).\tag{9}$$

An exact solution of equation (9), involving hyperelliptic integrals, will be discussed elsewhere. The solution of equation (9) is simple in the following two cases:

a)   When $\omega = 0$, that is, when the weight of the crown of the branch is large relatively to the weight of the supporting primary branch. Then

$$r^3(z) = \frac{4G}{\pi\,\sigma}\,(Y-z).\tag{10}$$

b)   When, on the contrary, $G = 0$, that is, when our primary branch is denuded of secondary branches, then equation (9) has the solution

$$r(z) = \frac{2\,\omega}{15\,\sigma}\,(l-z)^2,\tag{11}$$

as can be verified by substitution.

It should be noted that such a branch not only has no biological utility, but, as remarked by I. Opatowski (1945b, sec. 5), physically cannot exist. A calculation of its deflection leads to infinite values. This objection can be made whenever at the tip $r(z)$ is an infinitesimal of at least second order in $(l-z)$.

If we take equation (11) as a first approximation and substitute into the second member of equation (9), we get as a second approximation

$$r^3_1(z) = \left[\frac{2\,\omega}{15\,\sigma} \right]^3 (l-z)^6 + \frac{4G}{\pi\,\sigma} (Y-z). \tag{12}$$

We see that this approximation $r^3_1(z)$ is the sum of the two exact solutions (10) and (11) obtained by considering respectively the weight of the crown alone and the weight of the branch alone.

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OUTLINE OF A MATRIX CALCULUS FOR NEURAL NETS

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The activity of a neural net is represented in terms of a matrix vector equation with a normalizing operator in which the matrix represents only the complete structure of the net, and the normalized vector-matrix product represents the activity of all the non-afferent neurons. The activity vectors are functions of a quantized time variable whose elements are zero (no activity) or one (activity). Certain properties of the structure matrix are discussed and the computational procedure which results from the matrix vector equation is illustrated by a specific example.

Let a neuron be assumed to have the following properties. Its activity is of the "all or none" character. Unless it is an afferent neuron it can be brought into activity only by the action of other neurons which have terminal bulbs upon it, provided these act upon it all within the period of latent addition. Its activity lasts throughout its "time of action," beginning at the end of a synaptic delay. The synaptic delay is measured from the time at which sufficient conditions have first been met. More specifically, we shall assume that the synaptic delay time is the same for all neurons, and that compared with this, the period of latent addition, the time of action and the conduction times are negligible. For convenience this interval will be taken as the unit of time, and we shall treat time as being quantized.

By a synapse shall be meant the relationship between the terminal bulb of one neuron and a dendrite or cell body of another neuron. If such a synapse can activate the second neuron under any condition, it shall be referred to as an excitatory synapse and the terminal bulb as an excitatory bulb. If a synapse can ever prevent activity of the neuron acted upon, it shall be referred to as an inhibitory synapse with an inhibitory "bulb." We shall assume that one inhibitory synapse can act to neutralize the effect of one excitatory bulb in the same synapse group. Evidently total inhibition can be obtained by n^* inhibitory synapses where n^* is a number equal to or greater than the total number of excitatory synapses in the group of synapses acting upon a common neuron.

Let θ_k be the least number of excitatory terminal bulbs acting simultaneously upon neuron N_k, which is necessary for the neuron

to act a unit of time later.

Let $E^k{}_j$ be the number of excitatory bulbs from neuron N_j terminating upon neuron N_k, and $I^k{}_j$ the number of inhibitory bulbs, and let $B^k{}_j = E^k{}_j - I^k{}_j$.

Define

$$f_{jk} = B^k{}_j / \theta_k. \tag{1}$$

Evidently f_{jk} may be positive, negative, or zero. It is zero if $E^k{}_j = I^k{}_j$ or if N_j does not synapse with k, in which case $E^k{}_j = I^k{}_j = 0$.

Let the group of synapses implied in f_{jk} for all values of j form a synapse group on neuron k. Assume that for every synapse group the effects of all terminal bulbs is simply additive. If a subgroup did not add with the rest of the group but only added within itself, then the neuron k may be replaced by three neurons. Two of these, $N_{k'}$ and $N_{k''}$, are associated with the respective subgroups only and each acts on the third, which has a threshold less than the number of bulbs terminating on it either from $N_{k'}$ or $N_{k''}$. The third neuron acts upon the same set of neurons as does N_k. The time delay introduced can generally be compensated for in the rest of the net. If there are several subgroups which overlap, this introduces a more complex reduction. We shall hereafter assume that each neuron has but one afferent synapse group.

Let a net of n neurons be divided into afferents, efferents, and internal neurons. We shall only mean by an afferent a neuron not acted upon by any neuron in the net under consideration. Similarly an efferent is a neuron which does not act on any other neuron in the net. We may, however, refer to the afferents as receptors and the efferents as effectors. Let the ρ receptor neurons be N_1, N_2, $\cdots N_r$, $\cdots N_\rho$, the ι internals be $N_{\rho+1}$, $\cdots N_i$, $\cdots N_{\rho+\iota}$ and the ε effector neuron be $N_{n-\varepsilon+1}$, $\cdots N_e$, $\cdots N_n$. Define a structure matrix F as a square matrix having the row and column indices 1, 2, $\cdots n$ corresponding to the n neurons such that

$$F = |f_{jk}| =
\begin{array}{c|ccc}
 & 1...r... & \rho+1...i... & (n-\varepsilon+1)...e...n \\
\hline
1 & 0 & F_R & F_X \\
 & 0 & F_I & F_E \\
n & 0 & 0 & 0 \\
\end{array}
\tag{2}$$

Each element in row j determines which neurons are acted upon by neuron N_j and in what manner. Similarly each element in column k determines which neurons act upon N_k and in what manner. The matrices F_R, F_X, F_I, and F_E, appearing in equation (2), determine respectively the relationships receptor–internal, receptor–effector, internal–internal, and internal–effector. Define the matrix R as the $n \times n$ matrix, obtained from F by substituting zeros for all elements except those of F_R. Define in a similar way the matrices X, I, and E. We shall assume that no neuron acts upon itself so that $f_{kk} = 0$ for all k, and F and F_I have all diagonal elements equal to zero.

If any row α in F contains only positive or zero elements, then N_α is a purely excitatory neuron. If any row β in F contains only negative or zero elements, then N_β is a purely inhibitory neuron. If both positive and negative elements occur in a given row, the corresponding neuron may be referred to as a mixed neuron.

Define the $(1 \times n)$ row matrix or vector a, by

$$a(t) = (a_1, \cdots a_r, \cdots a_\rho, a_{\rho+1}, \cdots a_i, \cdots a_\iota, a_{n-\varepsilon+1}, \cdots a_e, \cdots a_n), \qquad (3)$$

where any element a_j is 1 or 0 depending on whether N_j does or does not act at the time t. The vector $a(t)$ may be referred to as the activity vector at the time t. This vector may be written as the sum of three $(1 \times n)$ vector components, r, i, e, the receptor, internal, and effector components having the respective set of elements a_r, a_i, and a_e only, and zeros elsewhere. The scalar quantity $v_k(t)$ given by the sum

$$v_k(t) = \sum_{j \varepsilon \beta} B^k{}_j / \theta_k, \qquad (4)$$

taken over a class β of neurons which is defined as the class of all neurons synapsing on N_k which are active at $t-1$, gives a measure of the net excitation affecting the neuron N_k. The quantity $v_k(t)$ may be expressed as

$$v_k(t) = \sum_{j \varepsilon \beta} f_{jk} = \sum_{j=1}^{N} a_j(t-1) f_{jk}, \qquad (5)$$

because of the definitions of f_{jk} and β. A vector $v(t)$, whose components for $k > \rho$ are the values of $v_k(t)$ and for $k \leq \rho$—the values of $a_k(t)$, can be expressed as

$$v(t) = r(t) + a(t-1)F. \qquad (6)$$

In order to normalize $v(t)$, let G be a post-operator on a row vector, such that, if $[v\,G]_k$ is the kth component of the vector $[v\,G](t)$,

$$[v \, G]_k = 1 \quad \text{if} \quad v_k \geqq 1,$$
$$[v \, G]_k = 0 \quad \text{if} \quad v_k < 1. \tag{7}$$

Since G operates only on a vector appearing just to the left of it, and not on a matrix, the expression $(vF)G$ may be written vFG. The parenthesis could not be eliminated if a pre-operator were used.

Equation (6) may now be written

$$a(t) = v(t)G = [r(t) + a(t-1)F]G. \tag{8}$$

The post-operator G will not in general be distributive with respect to vector addition. It is not associative with v and F. However, in equation (8) the vectors $a(t-1)F$ and $r(t)$ satisfy $[a(t-1)F]_k \times [r(t)]_k = 0$ for all values of k, in which case it can be readily seen that G is distributive. Also $rG = r$. Thus we have the following theorem:

The activity of any net represented by a structure matrix **F** *is determined from the afferent stimulation and its activity at the beginning of the prior interval of time according to the equation*

$$a(t) = r(t) + a(t-1)FG. \tag{9}$$

Equation (9) leads to the recursion formula

$$a(t) = r(t) + \{r(t-1) + \left[r(t-2) + \cdots \left[r(2) + [r(1) + \right. \right.$$
$$\left. \left. a(0)FG] \, FG \right] \cdots FG \right] FG\} \, FG. \tag{10}$$

The vector quantity between the first and last brackets in expression (10) is simply the vector $a(t-1)$.

Thus if the structure of a net is known together with a sequence of r's, $r(0), r(1), \cdots r(\tau - 1)$, and the initial activity of the internal neurons $i(0)$, it is possible from equation (10) to determine the activities of the net for any time t from 0 to τ, $a(1), a(2), \cdots a(\tau)$.

Because of the character of the structure matrix F, equation (9) may be written as a pair of equations

$$i(t) = [r(t-1)R + i(t-1)I]G, \tag{11}$$
$$e(t) = [r(t-1)X + i(t-1)E]G, \tag{12}$$

from which one may determine successively $i(t)$ and $e(t)$ for every t. For both $i(t)$ and $e(t)$ formulas similar to expression (10) can be written.

From equation (11) it is evident that the sequence of i's can be determined from a knowledge of the afferent–internal structure and

internal–internal structures, together with the sequence of afferent activities and an initial internal activity pattern. On the other hand, to determine the sequence of e's, that is, the pattern of the efferent activity, one must also know the rest of the structure of the net.

Every row and column of F, excluding the first ρ columns and last ε rows, contains at least one non-zero entry; otherwise, it represents an afferent or efferent. If only one non-zero entry occurs in any column, it may be replaced by unity, for if it is less than one, the neuron of the corresponding column can never act, and thus this neuron should be deleted. Furthermore, there is no restriction to set an element equal to one, if this element is greater than one.

For each term in the expansion of the determinant of F_I for which a class of q non-zero factors have subscript pairs forming a permutation of order q, there is a closed chain of q neurons. If each factor is ≥ 1, it is a functional closed chain. Let D_I represent any term in the expansion of the determinant of F_I in which zero elements of the term are omitted and the non-zero elements are written as f_{jk}. Then for every D_I in which any class of the subscript pairs forms a permutation, there corresponds to this a closed chain of neurons, the number of neurons being the same as the order of the subscripts. If M_p is the $p \times p$ matrix obtained from the matrix I by deleting all rows and columns except those associated with these p neurons, and if the expansion of the determinant contains only one non-zero term, then the closed chain is simple if the subscript pairs form a permutation of order p, and no proper part of this permutation is itself a permutation. Otherwise, each neuron is a member of a simple closed chain, each chain being disconnected with any other insofar as these p neurons are concerned. If each element f_{ij} within a permutation is ≥ 1, the closed chain is functional. If any row or column in I contains more than one non-zero entry, and each contains at least one non-zero entry, there is at least one complex closed chain or one pair of connected closed chains. If the $(\iota \times \iota)$ matrix F_I is a permutation matrix and if $r(0) = r(1) \cdots = 0$, then after a finite time the sequence of e's is cyclic and of order ι or some submultiple.

To give an example of the application of the present method, we exhibit the matrix for the circuit illustrated in Figure 1e of the paper by W. S. McCulloch and W. Pitts (1943):

		1 2	a b	3 4
1	$F=$	0	0 0	1 0
2			1 −1	0 $\frac{1}{2}$
a		0	0 1	0 $\frac{1}{2}$
b			0 0	1 0
3		0	0	0
4				

If the net is initially at rest, then according to W. S. McCulloch and W. Pitts the condition for the activity of neuron 3 at $t = 0$, is either that neuron 2 acts at $t = -3$ but not at $t = -2$; or that neuron 1 acts at $t = -1$. That is, the sequence of r's, writing only the a_r components, $r(-3) = (0, 1)$, $r(-2) = (0, 0)$, $r(-1) = (0, 0)$ as well as the sequence $r(-1) = (1, 0)$ is adequate to produce activity in neuron 3. We shall assume that $r(t) = 0$ for all $t \geq 0$. If $r(-3) = (0, 1)$ then from equation (9) $a(-2) = (0, 0; 1, -1; 0, \frac{1}{2})G = (0, 0; 1, 0; 0, 0)$, $a(-1) = (0, 0; 0, 1; 0, 0)$, and $a(0) = (0, 0; 0, 0; 1, 0)$, so that $e(0)$, writing only the a_e components is $e(0) = (1, 0)$, that is, neuron 3 acts but 4 does not. Similarly if $r(-1) = (1, 0)$ then from equation (9) $e(0) = (1, 0)$. Note that for both sequences $a(1) = 0$.

The condition for neuron 4 to act as $t = 0$ is that neuron 2 acts at $t = -2$ and at $t = -1$. If $r(-2) = (0, 1)$ and $r(-1) = (0, 1)$, then from equation (9) $a(-1) = (0, 1; 1, 0; 0, 0)$ and $a(0) = (0, 0; 1, 0; 0, 1)$, so that neuron 4 acts but 3 does not. Note that for this sequence $a(1) = (0, 0; 0, 1; 0, 0)$ and $a(2) = (0, 0; 0, 0; 1, 0)$ so that neuron 3 always acts as a unit of time after discontinuation of continuous stimulation of neuron 2.

In the above example unnecessary restrictions were imposed for simplicity. Evidently, if the net is initially at rest and x denotes a quantity which is either zero or one, then the sequence of r's given by $r(-3) = (x, 1)$, $r(-2) = (x, 0)$, $r(-1) = (x, x)$ or the sequence $r(-1) = (1, x)$ results in the efferent activity vectors $e(-2) = (x, 0)$, $e(-1) = (0, 0)$ and $e(0) = (1, 0)$ for the first sequence and $e(0) = (1, x/2)G = (1, 0)$ for the second. On the other hand, the stimulus pattern $r(-2) = (x, 1)$ and $r(-1) = (0, 1)$ results in

$e(-1) = (x, 0)$ and $e(0) = (0, 1)$.

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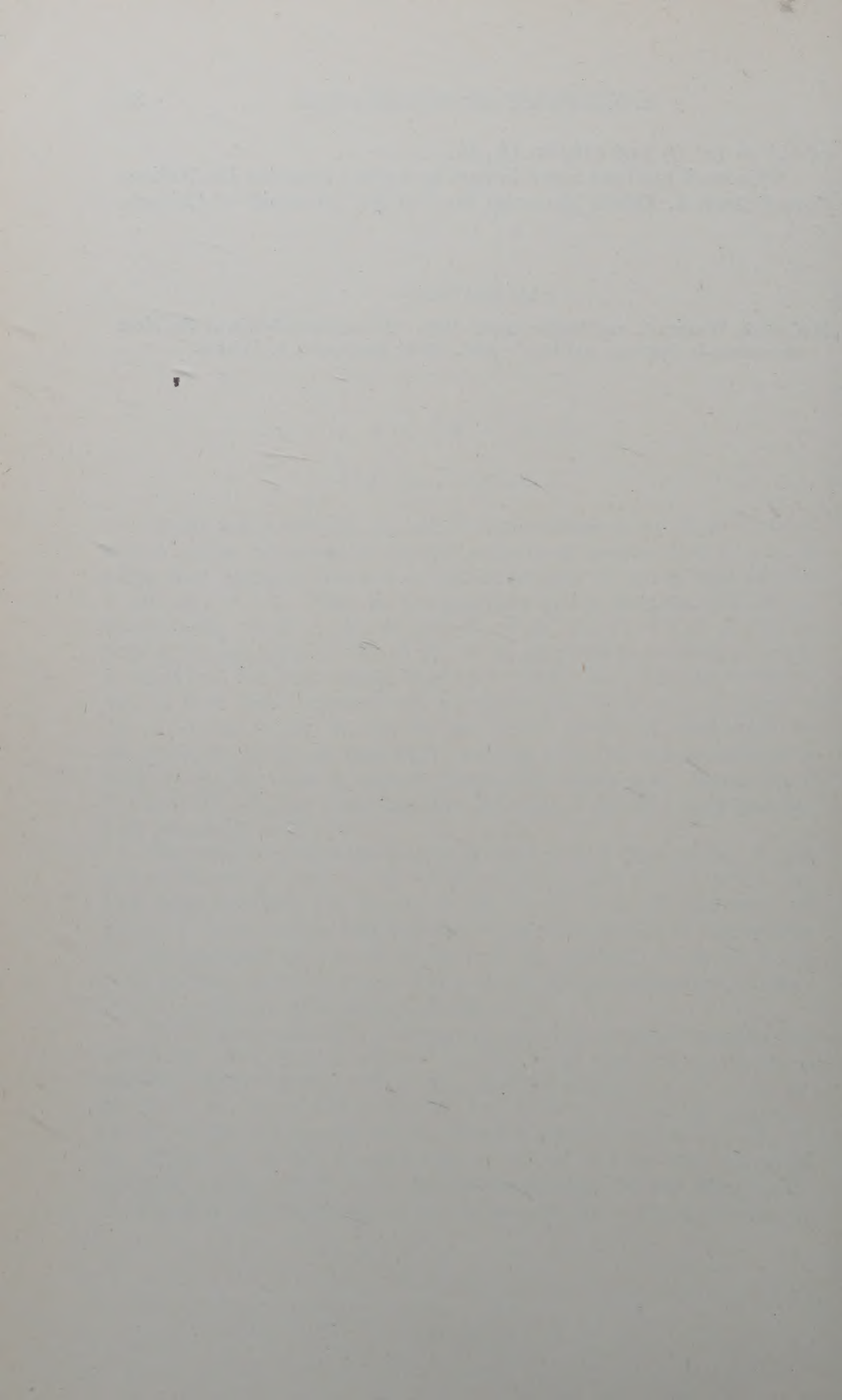
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